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THE BIOLOGY OF *ANTHOCORIS NEMORUM* (L.) IN SCOTLAND (HEMIPTERA: ANTHOCORIDAE).

By A. R. Hill.

(*Zoology Department, Glasgow University*)

Manuscript received 19th March, 1957.

(Read 1st May, 1957).

With 3 Text-figures.

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I. Introduction.

Within the past few years the importance of predators and parasites, in the ecology of orchards particularly, has come to be more fully appreciated and simultaneously our ignorance of the biology of many predaceous species has become very apparent. Thompson (1951) summed up the situation by saying that "An understanding of the behaviour of predaceous insects and more particularly of the specificity or non specificity of their host relations is therefore very necessary in any attempt to evaluate the importance of predators as controlling agents of injurious insects".

Although it has long been known that members of the genus *Anthocoris* are important predatory insects which attack, among other pests, aphids, thrips and red-spider, very little has been published in Britain on their biology. Butler's account (1923) of the species of this genus largely represents our present-day published knowledge. Peska (1931) described the life-history, feeding habits, etc., of *A. nemorum* in Poland. Collyer (1953) included brief references to this and other species in respect of the ecology of the fruit tree red spider mite. Sands' unpublished thesis (1954) contains most of the information so far collected but because of limitations of time the treatment is somewhat incomplete. This latter work was not brought to the author's attention until the present investigation was practically completed.

The observations now described yielded results differing in a number of respects from those reported by previous workers, and therefore justify their publication in the present paper.

II. Materials and Methods.

Adult specimens of *A. nemorum* were collected in the field as soon as they emerged from hibernation; with rare exceptions all were females. Each specimen was placed in a 3″ × 1″ flat-bottomed corked tube. A disc of moist filter paper was used to cover the inner surface of the cork. The paper disc was large enough to project from the rim of the tube in the form of a fringe when the cork was in position. This fringe permitted some evaporation of moisture from the filter paper to the outside atmosphere and reduced condensation within the tube to a minimum. The adult females readily accepted the moist paper for oviposition.

The tubes were examined twice daily, when the filter paper discs were renewed and the eggs were counted. A fresh supply of aphids for feeding purposes was added daily, and at the same time the numbers of aphids consumed during the previous twenty-four hours were recorded.

The tubes were all kept under the same conditions in a laboratory with a northern aspect where temperature fluctuations and seasonal temperature changes were minimal.

All measurements were made by means of an eye-piece micrometer on both preserved and living material. A camera-lucida was used for making drawings.

III. The Distribution of *Anthocoris nemorum* (L.).

Reuter (1885) stated that this species is found all over Europe, in Asia Minor, in the wooded areas of Siberia, Kamtschatka. He cited D. Frey Gessner as recording it from altitudes up to 3000 feet. Butler limits its European distribution at the 70° N. parallel and added all the palaearctic parts of north Africa to Reuter's list.

A. nemorum is undoubtedly the commonest and most widely distributed member of the genus in Great Britain. It has been recorded from all the counties in England and Wales except Northampton, Monmouth, Flint, Denbigh, Montgomery and Cardigan which have probably not been adequately searched. No detailed Scottish county distribution lists are yet available for Heteroptera, but *A. nemorum* appears to be widespread and common there too.

IV. Plants Inhabited by *A. nemorum*.

In addition to a wide geographical distribution, *A. nemorum* is found on many species of plants, an indication, no doubt, of its catholic taste in prey. Reuter stated that it was found on various plants and trees. Butler confirmed this and added that " it is also found on flowers and many low plants " and that it may play some part in their cross pollination. Butler gave a list of seventeen plants belonging to nine natural orders on which *A. nemorum* had been found, and in all cases the insects bore the pollen of the plants concerned. One of the common names for Anthocorid bugs is " Flower Bugs ". The following is a list of plants on which this insect has been found, compiled from past records, together with the author's own observations.

Thlaspi arvense L., *Moricandia arvensis* (L.), *Acer pseudoplatanus* L., *Aesculus hippocastanum* L., *Sarothamnus scoparius* (L.), *Rubus idaeus* L., *R. fruticosus* agg., *Crataegus monogyna* Jacq., *Pyrus communis* L., *Malus* sp., *Ribes nigrum* L., *Hedera Helix* L., *Pimpinella major* (L.), *Foeniculum vulgare* Mill., *Daucus carota* L., *Mercurialis perennis* L., *Euphorbia helioscopia* L., *Urtica dioica* L., *Betula verrucosa* Ehrh., *Alnus glutinosa* (L.), *Corylus avellana* L., *Fagus sylvatica* L., *Quercus robor* L., *Primula vulgaris* Huds., *Fraxinus excelsior* L., *Convolvulus arvensis* L., *Solanum tuberosum* L., *Lamium album* L., *Pulicaria* sp., *Aster tripolium* L., *Achillea millefolium* L., *Carduus crispus* L., *Cirsium arvense* (L.), *Taraxacum officinale* agg., *Triticum aestivum* L., *Hordeum* sp., various Gramineae.

V. Field and Laboratory Observations on the Life History.

(1) *Hibernation and Spring Emergence.*

The winter is passed by the insect in the adult stage, although some fifth instar nymphs have also been found in hibernation. The hibernacula are located in sheltered places such as under bark of trees, shrubs, in hollow plant stems, under stones, in cushions of moss, under fallen leaves, etc. It has been recorded also in a nest of *Bombus agrorum* Fab. According to Butler the species is active in all months of the year except November, January and February. During the present investigation active individuals have been found throughout the year except for the months of December, January and February. It is clear, therefore, that on rare warm days in winter this insect is capable of becoming active, deriving nourishment no doubt from ova of other insects, etc., and from any other small creatures which have also been activated by the rise in temperature.

The date of final emergence from hibernation depends on climatic conditions. The earliest date recorded during this investigation was 23rd March, while the latest was 16th April. Only very exceptionally are males found in the spring in Scotland. Fertilization occurs during the previous autumn and the vast majority of males die during the winter. Ovaries of females disected shortly after the spring emergence were found to be in an advanced state of development with the sperm receptacles full of spermatozoa. Oviposition commences approximately ten days after emergence.

(2) *Distribution of* A. nemorum *on Plants in the Spring.*

In early spring newly emerged adults favour *Salix* spp., where they find, like many types of insects, a ready supply of food. *A. nemorum* is, however, present in smaller numbers at an equally early date on *Sarothamnus scoparius* (L.), *Mercurialis perennis* L., *Crataegus monogyna* Jacq. and *Quercus robor* L. On hawthorn it is active when the buds are just bursting and on oak it has been found among the previous year's unfallen, dead leaves, long before bud burst. Under these conditions prey species are scarce and it would appear that ova and Collembola serve as the main source of food. For two or three weeks willows remain the most favoured plants, but migration to other plants soon takes place and the population on willows is reduced ; indeed the populations on hawthorn and oak surpass those on willow, and the insect also soon appears on other low-growing plants. By the end of April it has been collected in Scotland from *Alnus glutinosa* (L.), *Pyrus communus* L., *Malus* sp., *Rubus fruticosus* L., *R. idaeus* L., *Ribes nigrum* L., *Hedera Helix* L., *Lonicera periclymenum* L. and from various grasses, etc. In a short time the insect can be obtained from the wide variety of plants listed in the previous section.

The spring distribution of *A. nemorum* is governed by the distribution of prey species. Willows are favoured because, when most other trees are just at or approaching bud-burst, they are in full flower, displaying the conspicuous catkins which attract much insect life.

(3) *Oviposition.*

All observers are agreed that the oviposition period is an extended one. Peska noted oviposition by over-wintered females from 3rd April until the middle of June. Collyer recorded oviposition from the end of March until June, and added that in May and June imagines of both generations can be found together. Sands makes a similar statement, and the observations recorded here are in total agreement.

In nature the ova are inserted by the female into the tissues of the plant (usually leaf-tissue) just below the epidermis, so that only the white sculptured operculum is exposed. Under laboratory conditions the eggs were similarly placed in the moist filter paper in the tubes. They were inserted horizontally,

TABLE I.—*Length of life and egg-laying activities of ten females collected in the field and studied in the laboratory.*

Female No.	Length of life in days	Total No. of eggs laid	No. of eggs laid per week.								
			1	2	3	4	5	6	7	8	9
1	34	61	2	3	14	24	18	.	.	.	.
2	25	39	10	3	22	4	.	.	.	.	.
3	36	21	7	2	8	4	0	0	.	.	.
4	15	10	8	2	.	.	.	.	.	.	.
5	18	3	3	0	0	.	.	.	.	.	.
6	68	213	19	3	16	23	34	34	30	31	23
7	43	95	7	3	22	20	29	14	.	.	.
8	32	60	6	8	11	27	8	.	.	.	.
9	43	68	13	0	17	22	10	6	.	.	.
10	40	119	10	6	20	26	45	12	.	.	.

causing the paper to bulge into a small but clearly visible blister, which facilitated the location and counting of eggs. The operculum tends to face obliquely upwards because of the slight curvature of the egg (fig. 1*a*).

When about to oviposit the female walks slowly over the surface of the leaf, touching it every few seconds with the tip of her rostrum. At the same time her antennae are vibrating fairly rapidly ; only occasionally, however, do they appear to touch the leaf. Quite suddenly the female stands still, raises her body high and flexes the tip of her abdomen so that it touches the surface of the leaf. The ovipositor is then inserted into the leaf tissue, whereupon the abdomen then shows rhythmical contracting movements. The final passage of the ovum into the plant tissue takes place without any perceptible extra effort and the ovipositor is at once removed. The average time taken for oviposition was 110 seconds.

The maximum number of eggs laid by one female in a day was 10, but the average was 1·6. There was considerable variation in the numbers laid individually. Detailed records of ten females collected in the field as they emerged from hibernation and studied in the laboratory showed between 3 and 213 eggs laid (Table I). The female which laid the fewest eggs lived for only 18 days, while at the other extreme one female lived for 68 days. Peska (1931) gives detailed records of the spring egg-laying activities of three females and he too found considerable variation in the total numbers of eggs laid, 203, 96 and 55 being the figures recorded by him.

It is thus evident that the spring oviposition-period is a fairly extended one. The majority of females in the sample lived for at least five weeks and most of them oviposited (sometimes intermittently) over the entire period. Perhaps in the field it may not be uncommon for a significant proportion of the population to live and oviposit for as long a period as did female 6. This point is of some importance when voltinism is discussed.

The filter paper discs were examined and, if necessary, changed twice daily, in the morning and in the evening, to discover whether a diurnal oviposition rhythm existed. Out of a total of 689 eggs observed, 309 were laid during the day while 380 were laid at night. The difference is not significant and there is no clearly defined rhythm in the egg-laying activities of individual females.

Tests made from time to time showed no diminution in viability of the eggs, even of those laid in the ninth week by female 6. None of the females had had opportunity of spring copulation, so that all fertilization had been effected by the spermatozoa received during the previous autumn and stored in the sperm receptacles. Peska was of the opinion that fertilization occurred in the spring, while Sands indicated that multiple copulation was necessary. Neither of these obtains under Scottish conditions.

In a few instances it was noted that some females pierced and sucked their own eggs, leaving only the shrivelled, transparent chorion. Accompanying this was a further type of abnormal behaviour, namely the laying of eggs on the surface of the filter paper or on the glass of the tubes. At first it was thought that shortage of food might be the cause of this behavioural aberration, but it continued to occur even in the presence of abundant food. No difference could be detected in the condition of the filter paper discs ; indeed in most cases eggs were inserted normally into the paper as well as on the surface. The sucking of the ova may be a normal response of *A. nemorum* to finding exposed eggs

whether they be of its own or of another species. This peculiar habit was observed during one year out of the three for which detailed records were kept.

(4) *Description of the Ovum.*

The ovum is elongate and somewhat curved. At one end it is slightly swollen and evenly rounded, while at the other end there is a sculptured operculum (fig. 1*a*). At first the egg is opalescent but it undergoes colour changes during development. A faint pattern of polygonal areas can be detected on the surface.

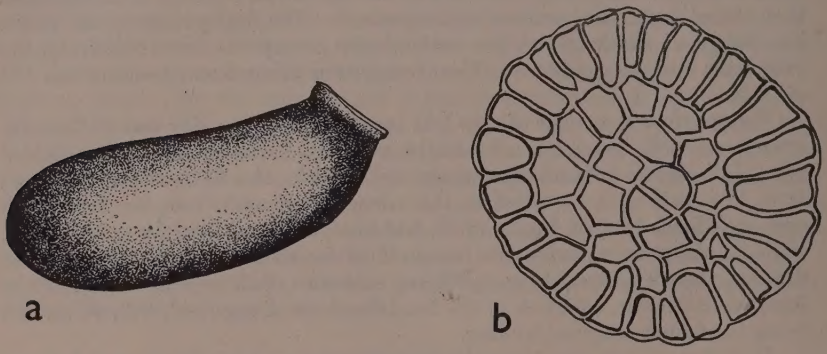

Fig. 1.—(*a*) Ovum of *A. nemorum*, lateral view, × 100. (*b*) Operculum of ovum of *A. nemorum*, × 400.

The operculum is chalky white in appearance and roughly circular in outline, with its outer margin showing a ring af narrow rectangular areas set radially. The rim occupies about half the area of the operculum (fig. 1*b*). The central zone is roughly circular and shows small irregular-shaped areas of varying size.

The mean dimensions of the ovum are : length 0·783 mm.; width, 0·277 mm.; diameter of operculum 0·156 mm. These dimensions are somewhat smaller than those recorded elsewhere.

(5) *The Incubation Period.*

The majority of eggs hatch after an incubation period of approximately seven days but the period ranges between six and eleven days under identical physical conditions (fig. 2).

During development there are marked colour changes in the ovum. Whereas on the first day the egg is almost colourless and opalescent, showing only a suspicion of a very pale orange tinge, this tinge becomes stronger and more extensive during the second day until, towards the end of that day, the posterior two-thirds of the egg are pale orange distinctly visible to the unaided eye. Early on the third day the whole egg is orange coloured but the anterior third is still much paler than the rest. About one third of the distance back from the operculum, and at the extreme posterior tip, deep orange coloured concentrations are visible. By the fourth day these have spread so that about half of the egg is orange coloured, and towards the end of the same day they form two distinct zones, one occupying the posterior half of the egg and the other forming a

zone just behind the operculum from which it is separated by a narrow pale zone ; a broader pale orange zone separates the two deep orange zones from one another. By the fifth day the entire egg is orange in colour, the pale areas having disappeared, while the deep orange zones are now *vermilion*. This condition gradually changes during the sixth day until the egg is of a unifomly deep orange colour, the *vermilion* regions having contracted markedly to form a sub-opercular zone and a mid-ventral spot. The pigmented eyes are now visible through the chorion. In this condition the egg is ready to hatch.

(6) *Eclosion.*

Immediately prior to hatching the embryo performs vigorous movements so that it is able to free itself, still enclosed in the chorion, from the surrounding plant tissue. By these activities the egg may come to stand perpendicular to

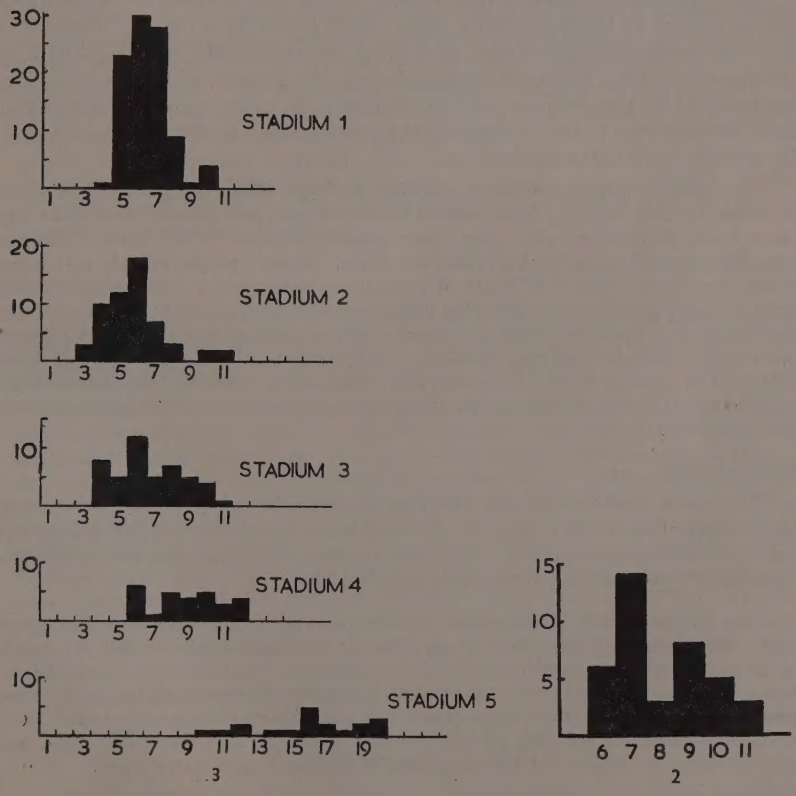

FIG. 2.—Frequency distribution histograms of the incubation period. *Abscissa*, time in days ; *ordinate*, number of observations.

FIG. 3.—Frequency distribution histograms of durations of instars 1 to 5. *Abscissae*, time in days ; *ordinates*, numbers of observations.

the surface of the leaf, still showing the slight curvature already noted. At this stage the operculum is still in position and slow bending or dorso-ventral levering movements continue until, after three or four minutes, it suddenly drops off, after which the embryo comes to lie at an obtuse angle to the leaf surface and all efforts are now directed to freeing the appendages from the chorion. After about 90 seconds the antennae are extended and in another 20 seconds all the legs are free. Muscular movements of the abdomen gradually free it from the chorion. The last stage is accomplished by the nymph bending forward and grasping the substratum in front and, this extra purchase having been gained, only a few seconds are needed for the insect to free itself completely. The average time taken is 7 minutes.

(7) *Description of Instars, their Duration and the amount of Food consumed.*

First Instar.

Under identical conditions the duration of the first stadium of 96 specimens ranged from 4 to 10 days, with a mean value of 6·3 days (fig. 3). Records of 94 of these nymphs showed that each killed between 3 and 12 aphids, with an average kill of 5·9. In the majority of cases the number of aphids killed was proportional to the duration of the stadium. In a few instances, however, a small number was killed by individual nymphs which showed a long stadium. In all cases food was abundant.

On hatching, a minute creature of a brilliant vermilion colour emerges which in a very short time darkens slightly. *Head* medium red-brown with pale sutures. Antennae: segments I–III colourless or very pale straw coloured, segment IV red brown. Rostrum colourless proximally, grey black on distal two-thirds. *Thorax:* pronotum, light red; mesonotum grey brown, about half length of pronotum; metanotum a uniform straw colour equal in length to mesonotum but wider than both the mesonotum and pronotum; a pale longitudinal line distinctly visible traversing all three segments in a mid-dorsal position. *Legs* mainly colourless, tarsi grey. *Abdomen* a fairly uniform red-brown but with mid dorsal two-thirds of segments I–III a deeper red and corresponding region on remaining segments very slightly paler than lateral regions. Body very sparsely covered with hairs less distinct than those on antennae.

Second Instar.

The mean duration of this stadium was 5·3 days but individual records ranged from 3 to 11 days (fig. 3). From 3 to 12 aphids were killed during the stadium, the mean being 6·1; there was a more constant correlation between duration of stadium and number of aphids killed.

Head, red-brown with sutures paler; eyes red-brown but of a darker hue than rest of head. Antennae: segments I and II colourless or very pale straw coloured, III mainly pale straw coloured but distal one-eighth light red-brown, IV red. Rostrum grey. *Thorax*: pronotum uniformly red-brown; mesonotum red-brown, becoming slightly paler along posterior border; metanotum yellow-brown with a red-brown suffusion on anterior third. A pale mid-dorsal line traverses all these thoracic segments. *Legs* very pale yellow, tarsi grey. *Abdomen* red-brown, but lateral margins of segment I paler than the rest.

Third Instar.

The third stadium averaged 6·6 days, but some individuals passed through it in 4 days, while others required 11 days (fig. 3). The numbers of aphids killed by nymphs at this stage ranged between 5 and 20 with the mean at 9·1.

Head, dark red-brown, (*i.e.* of a somewhat deeper hue than in earlier instars) ; sutures pale ; eyes, dark red-brown. Antennae : segment I grey-black, II pale straw coloured, III pale straw coloured with distal one-sixth light red, IV red-brown. Rostrum very dark grey, almost black except proximally, where it is red. *Thorax* : pronotum dark red-brown ; mesonotum dark red-brown, widening posteriorly ; metanotum, median two-thirds brown-red, the wing-pads pale straw coloured to white ; a pale mid-dorsal line present on all thoracic segments. *Legs* pale yellow, tarsi grey-black. *Abdomen* a uniform deep red-brown colour.

Fourth Instar.

The average duration of this instar was 8·9 days, the range being from 6–12 days (fig. 3). The mean number of aphids killed per nymph was 13·5 with a range from 6–27.

Head dark red-brown with pale red sutures ; eyes nearer general colour of head than in previous instars. Antennae : segment I dark brown, almost black, II pale straw coloured, III pale straw coloured with distal one-fifth dark red-brown, IV dark red-brown to pitchy. Rostrum pitchy except at base where it is pale laterally with a median, broad, dark longitudinal band. *Thorax* : pronotum dark red-brown, side slightly explanate or ridged ; mesonotum somewhat darker than head and pronotum, wing pads cream coloured ; median two-thirds of metanotum deep red-brown, wing pads paler than those of mesonotum ; a fine, median pale red line traverses the thoracic segments dorsally ; a fine, pale scattered pubescence visible dorsally on thorax. *Legs* : femora smoky grey-brown, paler at distal extremities ; tibia pale yellow, tarsi smoky grey, as femora, paler proximally. *Abdomen* dark red brown, darker than head and thorax except for segments I and II which are paler, with a fine, pale, scattered pubescence.

Fifth Instar.

The mean duration of this stadium was 16·35 days, but a range between 10 and 21 days was recorded (fig. 3). During this stadium on an average 24·05 aphids were killed, the range being between 16 and 33.

Head dark red-brown with pale sutures ; eyes wine red. Antennae : segment I dark brown, II testaceous, III testaceous with distal one-fifth dark red-brown, IV dark brown, darker than general body colour. Rostrum as described for fourth instar. *Thorax* : all three segments of same dark red-brown colour as head with the pale narrow median longitudinal line traversing them ; pronotum markedly trapezoidal in shape, margins explanate and narrowly pale brown, postero-lateral corners also pale brown ; mesonotum showing the wing-pads a creamy yellow ; metanotum largely hidden by the mesonotum but also showing cream-coloured wing-pads. *Legs* : femora smoky grey-brown, remainder pale straw coloured except for tarsi, which are very dark brown or black, each of the two segments somewhat paler proximally (especially in the third pair). *Abdomen* mainly red-brown, segment I honey-coloured and segment II somewhat paler than remainder of abdomen, segment IV with a pale area mid-dorsally. The insect covered by a fine pubescence.

Dimensions of all immature stages as in Table II.

(8) *Description of Adult.*

Head : black, shiny with slight tuberculation on antero-dorsal region ; sparsely pubescent, eyes deep red-brown, two ocelli somewhat paler in colour than compound eyes. Antennae : segment I pitchy, II testaceous except for distal one-third which is pitchy, III, proximal three-fifths testaceous, distal two-fifths pitchy, IV entirely pitchy ; all antennal segments beset with a fine, pale pubescence. Rostrum entirely pitchy. *Thorax* : Pronotum black,

TABLE II.—*Dimensions of immature stages.*

Instar No.	Specimen No.	Length of head.	Width of head.	Lengths of antennal segments. I.	II.	III.	IV.	Total.	Length of rostrum.	Length of pronotum.	Width of pronotum.	Length of abdomen.	Total length.
1	1	0·27	0·27	0·08	0·12	0·08	0·20	0·48	0·38	0·19	0·28	0·60	1·14
	2	0·28	0·27	0·09	0·14	0·09	0·21	0·53	0·43	0·17	0·30	0·58	1·15
	3	0·28	0·25	0·18	0·12	0·09	0·20	0·59	0·39	0·16	0·28	0·58	1·15
	4	0·22	0·24	0·07	0·14	0·11	0·20	0·52	0·41	0·16	0·27	0·58	1·09
	5	0·22	0·25	0·07	0·12	0·11	0·24	0·54	0·41	0·16	0·30	0·55	1·11
2	1	0·33	0·31	0·07	0·22	0·17	0·25	0·71	0·55	0·27	0·35	0·92	1·85
	2	0·35	0·32	0·07	0·22	0·17	0·25	0·71	0·51	0·25	0·35	0·92	1·81
	3	0·31	0·30	0·08	0·20	0·16	0·27	0·71	0·51	0·20	0·35	0·94	1·63
	4	0·36	0·33	0·07	0·22	0·16	0·25	0·70	0·55	0·27	0·39	0·92	1·81
	5	0·31	0·31	0·08	0·19	0·16	0·25	0·68	0·52	0·24	0·38	0·82	1·63
3	1	0·42	0·38	0·07	0·31	0·23	0·31	0·92	0·65	0·23	0·42	1·11	2·15
	2	0·42	0·38	0·08	0·27	0·23	0·34	0·92	0·57	0·31	0·42	1·07	1·96
	3	0·42	0·38	0·08	0·27	0·19	0·27	0·81	0·65	0·27	0·46	1·15	2·03
	4	0·42	0·38	0·07	0·31	0·19	0·31	0·88	0·57	0·23	0·46	1·07	1·96
	5	0·38	0·38	0·07	0·31	0·19	0·31	0·88	0·61	0·27	0·50	1·07	1·96
4	1	0·46	0·42	0·15	0·38	0·28	0·38	1·19	0·84	0·31	0·57	1·31	2·65
	2	0·50	0·42	0·12	0·38	0·31	0·38	1·19	0·76	0·38	0·57	1·34	2·69
	3	0·53	0·46	0·12	0·38	0·31	0·38	1·19	0·76	0·38	0·65	1·53	2·89
	4	0·46	0·42	0·12	0·38	0·31	0·38	1·19	0·81	0·38	0·57	1·38	2·69
	5	0·46	0·46	0·12	0·38	0·31	0·38	1·19	0·81	0·34	0·61	1·35	2·65
5	1	0·57	0·50	0·17	0·53	0·38	0·42	1·50	0·76	0·46	0·81	1·70	3·30
	2	0·53	0·53	0·20	0·53	0·38	0·42	1·53	1·07	0·42	0·84	1·84	3·46
	3	0·50	0·50	0·20	0·50	0·38	0·42	1·50	0·84	0·42	0·76	1·70	3·23
	4	0·53	0·53	0·16	0·50	0·34	0·42	1·42	1·07	0·46	0·84	1·76	3·34
	5	0·53	0·53	0·16	0·50	0·38	0·42	1·46	1·07	0·50	0·81	1·86	3·46

shiny, base deeply sinuate, lateral margins very slightly sinuate, anterior angles rounded behind apical collar, which shows distinct transverse striations; a smooth raised callosity present behind the collar, and reaching to middle region of pronotum, behind which is a groove with well defined striations; similar markings cover most of remainder of pronotum; a fine, pale pubescence present on pronotum, but very sparse on callosity. Scutellum black with pubescence as on pronotum; a deep transverse sulcus traverses middle of scutellum and posterior to it the surface shows fine transverse striations. *Elytra* entirely shiny with a pale, somewhat indistinct pubescence, except on cuneus, where it is golden and more distinct; clavus testaceous with proximal angle slightly darker than the rest and distal quarter dark brown, especially along suture margin. Corium very pale testaceous, almost transparent, and often showing a pale green hue, except on distal third, which shows an oval dark brown spot; embolium pale testaceous and almost transparent, darkening somewhat distally; cuneus, inner angle testaceous, darkening progressively towards margin of membrane and slightly paler brown along costal margin; membrane pale with a smoky zone, varying somewhat in shape and extent but somewhat like an hour-glass in many specimens, extending from the tip anteriorly over distal two-thirds of the membrane. *Legs* testaceous, except for a narrow band on proximal region of tibia and pretarsus, which are dark brown. *Colour*: Considerable variation occurs especially in depth of colour of darker areas of hemielytra. Dark area of cuneus sometimes extending to engulf dark spot at tip of corium; proximal dark ring on tibia more clearly defined and more extensive in some specimens than in others and a distal femoral dark ring occurs with varying distinctness, particularly on posterior pair of legs.

TABLE III.—*Dimensions of adult males and females.*

Specimen No.	Length of head.	Width of head.	Lengths of antennal segments. I.	II.	III.	IV.	Total.	Length of rostrum.	Length of pronotum.	Width of pronotum.	Length of scutellum.	Length of * elytra.	Total length.
1	0·50	0·53	0·19	0·69	0·42	0·50	1·80	1·15	0·57	1·19	0·57	2·23	3·87
2	0·57	0·50	0·23	0·61	0·42	0·50	1·76	1·07	0·53	1·03	0·57	2·11	3·78
3	0·61	0·53	0·19	0·69	0·38	0·46	1·72	1·19	0·57	1·19	0·65	2·46	4·29
4	0·57	0·53	0·19	0·69	0·46	0·53	1·87	1·19	0·61	1·21	0·69	2·42	4·29
5	0·57	0·53	0·19	0·69	0·46	0·50	1·84	1·15	0·57	1·15	0·69	2·34	4·17
1	0·53	0·51	0·15	0·61	0·38	0·42	1·56	1·11	0·53	1·15	0·57	2·34	3·97
2	0·57	0·55	0·15	0·65	0·46	0·50	1·76	1·19	0·57	1·30	0·65	2·57	4·36
3	0·53	0·53	0·15	0·65	0·46	0·48	1·74	1·03	0·53	1·11	0·57	2·26	3·89
4	0·57	0·55	0·19	0·61	0·42	0·50	1·72	1·15	0·57	1·26	0·61	2·42	4·17
5	0·57	0·53	0·17	0·61	0·42	0·46	1·66	1·11	0·57	1·26	0·61	2·42	4·17

(* measured from posterior tip of the scutellum to tip of the membrane.)

For nineteen individuals, complete records were obtained of the duration of the various stadia and the numbers of aphids consumed during each stadium (Table IV). It is at once clear that there is considerable variation in developmental times, even under identical conditions. The time range is further extended when batches reared at different seasons are compared. Those specimens which completed their development, excluding the incubation periods, by the last week of July (Table IV, Nos. 1–11) did so in 42–56 days (47·2 days mean) ; those developing from eggs laid later and reaching the adult form at the end of August (Table IV, Nos. 12–19) did so appreciably more rapidly, taking between 34 and 44 days (40·5 days mean). There was no significant difference between the rate of development of males compared with females.

There was no close correlation between the length of the immature period and the numbers of aphids consumed. While it is true that the individual which showed the longest developmental time also consumed the greatest number of aphids, yet another specimen ate as many aphids in approximately four-fifths of that time.

There is no indication that if development is slow during one stadium it is slow during all the stadia, for almost all the specimens examined showed that one stadium might be of short duration while succeeding stadia might be either near to the mean or extra long. This occurred in spite of ensuring that all nymphs received equal quantities of food in abundance. Malnutrition is unlikely to have been an important factor determining their variability.

VI. Food and Feeding Behaviour.

A. nemorum feeds on a wide variety of prey. It would appear to be mainly carnivorous, although reports exist of its feeding on plant juices. Prohaska (1923) suggested that the species sucks juices from the willow catkins and added that during much of the summer it sucks plant juices. Peska (1931) showed that it does not, in fact, feed on the catkins but rather searches out and feeds on small unspecified insects secreted under scales on catkins. Theobald (1895) indicated that *A. nemorum* can cause an appreciable amount of damage to hops and, with its congener *A. confusus*, is known to hop growers as the needle-nosed flea. During the present study there was no evidence that the species feeds to

TABLE IV.—*Showing in column (a) duration of various stadia and in column (b) the numbers of aphids consumed per stadium by developing nymphs of* A. nemorum.

Specimen number.	Incubation period in days	Stadium number. 1 (a)	1 (b)	2 (a)	2 (b)	3 (a)	3 (b)	4 (a)	4 (b)	5 (a)	5 (b)	Totals. (a)	Totals. (b)
1	6	7	5	6	6	8	6	9	11	20	22	50	50
2	7	6	4	6	7	7	11	7	13	21	24	47	59
3	7	8	6	3	4	6	9	11	17	18	29	46	65
4	6	5	4	5	4	9	9	9	14	18	19	46	50
5	6	6	5	4	6	10	7	9	10	18	20	47	48
6	6	6	3	6	7	8	6	9	14	15	16	44	46
7	9	7	3	7	10	5	7	8	16	15	21	42	57
8	9	7	5	10	11	9	17	11	19	19	25	56	77
9	8	8	10	7	8	8	12	8	17	16	16	47	63
10	7	4	3	6	6	9	8	10	9	16	19	45	45
11	6	6	5	11	12	6	10	6	10	21	29	50	66
12	4	4	4	7	5	10	10	10	23	12	21	43	63
13	4	6	4	6	3	6	5	10	25	16	22	44	59
14	6	6	5	5	5	6	15	10	11	17	31	44	67
15	.	6	3	5	4	5	12	6	15	12	28	34	62
16	.	6	5	5	4	6	10	8	10	17	31	42	60
17	.	5	3	5	6	7	19	8	16	15	33	40	77
18	.	6	5	7	6	6	11	6	9	17	33	41	64
19	.	7	6	6	5	4	10	6	10	13	25	36	56

any marked extent upon plant juices ; indeed it has been clearly shown that the entire life can be accomplished on a purely carnivorous diet.

Although *A. nemorum* feeds mostly on small arthropods such as Collembola, Aphididae, Thysanoptera, Acarina, etc., it has been observed to attack larger prey, such as medium sized lepidopterous larvae.

The following list of prey is compiled from the author's observations, and the records of a number of other workers: Collembola, Thysanoptera, Psocoptera, Miridae (nymphs and adults), Cicadidae, *Typhlocyba tenerrima* H-S., *T. ulmi* (L.), *T. cruenta* v. *douglasi* Ed., *Empoasca flaviscens* (Fab.), *Psylla mali* Sch., *P. pyri* L., *Arytaina genistae* (Lat.), *Macrosiphum rosae* (L.), *Acyrthosiphon onobrychidis* (Fonsc.), *Amphorophora rubi* (Kalt.), *Myzodes lonicerae* Mord., *Cryptomyzus ribis* (L.), *Brevicoryne brassicae* (L.), *Doralis fabae* (Scop.), *Eriosoma lanigerum* (Haus.), *E. ulmi* (L.), *Tetraneura ulmifoliae* Bak., *Cnaphalodes strobilobius* (Kalt.), *Conwentzia psociformis* (Curt.), larval Lepidoptera, *Apatura iris* (L.), *Hyponomeuta evonymella* (L.), larvae of *Lithocolletis* sp., larvae and pupae of *Anthonomus pomorum* (L.), dead *Rhyzotragus* sp., *Oligota flavicornis* B. & L., *Stethorus punctillum* (Wei.), cecidomyid larvae, tachinid larvae, *Metatetranychus ulmi* (Koch) (all stages), *Tetranychus telarius* L. (all stages), small spiders.

Adults and nymphs of *A. nemorum* also show cannibalism, as noted by various observers. During the present investigation adults were seen feeding on their own ova (see above), on nymphs of various ages and on other adults of their own species. On one occasion two late instar nymphs were found feeding on an adult.

When about to attack its prey, *A. nemorum* extends its rostrum horizontally, depresses the anterior part of its body, applies the tip of the rostrum to the integument of the prey and very quickly insinuates its stylets. The prey frequently walks away from the bug, which follows, its stylets still securely inserted. There is no clear evidence that the prey is paralysed by the secretions injected, and certainly paralysis does not occur rapidly ; nevertheless, after a short period, the movements of the prey become slower. It is interesting to note that *A. nemorum* can catch and retain such active prey as adult Psyllids.

VII. Copulation.

As already stated, copulation occurs during the late summer and autumn. Spring copulation was never observed during the present investigation. When a male encounters a female he at once attempts to mount on her back. This is frequently resisted and a vigorous struggle ensues, especially when the female has already been fertilised.

If the male succeeds in mounting, he rests on the back of the female and to her right side with his left tarsi hooked over the left margin of her pronotum and elytra, the anterior over the pronotum, the middle over the embolium region and the posterior over the membrane. The right anterior leg of the male is placed over the anterior edge of the face of the female, while the other two legs on the right side are extended to reach the substratum.

During the entire act of copulation the antennae of the male perform rapid forward and backward semaphore movements, working alternately and also showing a slight raising and lowering motion. Although closely watched the antennae of the pair were very rarely seen to touch.

While copulation is in progress the female remains quiet and moves very little. She normally stands with the anterior end depressed and the posterior end slightly raised. Her antennae are motionless or at most make very slight irregular movements from time to time. Occasionally the female takes a few steps, but for the most part she remains motionless.

The average time taken for the act was 7·5 minutes.

VIII. Number of Generations per Annum.

Hitherto it has been accepted that, in Britain, *A. nemorum* has two generations per annum (Butler, Collyer, Sands, etc.), though Collyer suggested that " a partial third generation could develop ; the first generation imagines begin to appear in May, the second in early July and this allows for a third and over-wintering generation in August and September. Although from data obtained this is obviously possible, there is yet no proof that it occurs in the field ".

Collyer stated that probably females only emerge in the spring, although in 1948 large numbers of both sexes were noted and copulation was common. Likewise Sands observed that in some years males are more common in the spring than in other years. He also recorded that one female in five was found to be unfertilized, with the ovaries in a very immature state. Southwood and Scudder (1956), stated that eggs laid by females towards the end of September give early instar nymphs at the beginning of October, which become adults in early November. In favourable years these adults are numerous and over-winter before pairing. In the following spring exceptionally large numbers

of males are found. Southwood and Scudder do not, however, base their evidence for this third generation on individual breeding experiments. More intensive study of the species in late summer and early autumn is therefore still required. It is nevertheless highly probable that a third generation does occur, at least in the south of England, for it is an established fact that *A. nemorum* has three generations per year in France (Bonnemaison and Missonier, 1956.)

The present investigation relates to a more northern latitude than those in which previous work has been done and shows clearly that in Scotland a univoltine race of *A. nemorum* exists. Specimens emerging from hibernation in late March or early April were almost all females. The proportion of males found was extremely small, indeed only three have been collected, one in late March, one in early April and one in early May.

Dissection of newly emerged females revealed that their sperm receptacles were filled with spermatozoa received at copulation during the previous late summer and autumn. While spring copulation may occur under Polish conditions as stated by Peska, it appears to take place only infrequently in England, while in Scotland it must be practically non-existent.

In Scotland, the first adults to develop from ova laid in early spring appear in the field during the last week of July or the first week of August, depending upon the climate. These dates are considerably later than any so far recorded in England or on the continent. Collyer stated that approximately 30–35 days are required for development from egg to final moult, so that the first adults appear in May. Likewise Sands records the period as just over 30 days, while Peska gives 26–34 days.

The developmental time of the northern race is markedly longer. Even under the equable and favourable conditions of the laboratory, the minimum time was 50 days, while the maximum was 65 days. Field observations show that under natural conditions the developmental period is even longer. For two of the seasons during which detailed records were kept the periods were 93 and 97 days. The overwintering adults were active between 16th April and 6th July and between 26th March and 6th July. After 6th July no adults were to be found in the field until 8th August and 26th July respectively.

A further indication that a univoltine northern race exists is provided by the dates of occurrence of males in the field. As already stated, one male specimen has been collected in each month—March, April and May; the May record was for the 6th May, and therefore all three dates are too early for the specimens to be other than overwintered males. Moreover, apart from these three overwintered males, none ever appeared until the last week of July, after which the male population increased steadily. It is considered certain that, under northern climatic conditions, the occurrence of a further generation during the late summer and early autumn would be impossible.

Final proof that the adults occurring after the end of July do not reproduce until the following year was obtained by dissecting female specimens at intervals until early October. In the vast majority of cases the sperm receptacles were filled with spermatozoa (copulation was frequently observed), but the ovaries were small and remained so, while the fat body steadily enlarged. In this condition the females went into hibernation and remained more or less comatose until the following spring.

The precise geographical range of the univoltine race is still under investigation.

IX. The Economic Importance of *A. nemorum*

Apart from the instances of damage to plants reported by Theobald, it would seem that *A. nemorum* is wholly beneficial. This investigation has shown the insect is capable of killing many aphids, and the figures given here fall far short of those published by Peska, who observed that an average of 248 aphids were consumed per individual bug during development. When the adult life period is included each bug was reported to consume an average of 500–600 aphids.

Collyer has stated that *A. nemorum* is an important predator in commercial orchards. She reported that its average consumption of fruit tree red spider mite per day is 50 adult females (although as many as 45 adults have been observed to be consumed in one hour). Nymphs of *A. nemorum* account for an average of 20–40 red spider mites per day, according to the insect's stage of development. In addition to attacking these mites in summer, it actively destroys many of their eggs in spring and autumn. *A. nemorum* has been recorded as an active predator on this mite in Finland, Germany, Great Britain, Holland, Norway, Russia and Switzerland (Collyer). Its importance as a controlling agent was pointed out by Massee and Steer as early as 1929. Within the past decade, with the introduction of new and highly potent insecticides, this has been even more clearly realised, and extensive investigations have been carried out in various countries to assess the effect of new insecticidal programmes on the predaceous faunas of crop plants. The importance of such predators in controlling pest populations has already been shown. Much further investigation is required into the use of insecticides which cause a minimum amount of harm to beneficial insects while giving a good measure of control of pest species. Indeed the most efficient method may well prove to be one which fully utilizes the combined action of chemicals and predators.

X. Summary.

The geographical distribution of *A. nemorum* is outlined and observations are made on the plant species inhabited by it. An account is given of laboratory studies of the life-cycle and comparisons are made with field observations under Scottish conditions. The various stages in the life-history are described. From this study it emerges that a northern race of the species exists which has only one generation per annum, instead of the two or three clear generations so far reported in the literature for regions farther south. At present no information exists as to the southern limits of this univoltine race. Observations are made on the feeding habits and prey of the species and its economic importance as a beneficial insect is indicated.

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